VEGETATION CHARACTERISTICS IMPORTANT TO COMMON SONGBIRDS IN EAST TEXAS

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Multivariate studies of breeding bird communities have used principal component analysis (PCA) or several-group (three or more groups) discriminant function analysis (DFA) to ordinate bird species on vegetational continua (Cody 1968, James 1971, Whitmore 1975). In community studies, high resolution of habitat requirements for individual species is not always possible with either PCA or several-group DFA. When habitat characteristics of several species are examined with a DFA the resultant axes optimally discriminate among all species simultaneously. Hence, the characteristics assigned to a particular species reflect in part the presence of other species in the analyses. A better resolution of each species' habitat requirements may be obtained from a two-group DFA, wherein habitats selected by a species are discriminated from all other available habitats.

Analyses using two-group DFAs to compare habitat used by a species with habitat unused by the same species have the potential to provide an optimal frame of reference from which to examine habitat variables (Martinka 1972, Conner and Adkisson 1976, Whitmore 1981). Mathematically (DFA) it is possible to maximally separate two groups of multivariate observations with a single axis (Harner and Whitmore 1977). A line drawn in three or n-dimensional space can easily be positioned to intersect two multivariate means (centroids). If three or more centroids for species are analyzed simultaneously, a single line can no longer intersect all centroids unless a perfectly linear relationship exists for the species being examined. The probability of such an occurrence is extremely low. Thus, a high degree of resolution can be realized when a two-group DFA is used to determine habitat parameters important to individual species. We have used two-group DFA to identify vegetation variables important to 12 common species of songbirds in East Texas.

METHODS

Four pine and four pine-hardwood stands representing growth stages from small sapling to sawtimber were selected for bird and habitat sampling. All stands were in the loblolly pine (*Pinus taeda*)-shortleaf pine (*P. echinata*)-hardwood forests of East Texas within an 80-km radius of Nacogdoches. Stands are described more completely in Dickson and Segelquist (1979) where the same bird data used in this study were used to examine bird diversity and density in relation to foliage layers.

A 10-ha study area within each stand was delineated away from adjoining habitats to

TABLE 1

HABITAT VARIABLES FOR 12 SONGBIRDS IN EAST TEXAS PINE AND PINE-HARDWOOD
FORESTS

Habitat variable	Code	Bird species	Code	N[a]
Vegetation height (m)	VEGHT	Carolina Chickadee	CCHK	37
No. shrub species	NSRSP	(*Parus carolinensis*)		
No. tree species	NTRSP	Tufted Titmouse	TUF	50
No. shrub stems	SRDEN	(*P. bicolor*)		
% canopy closure	CANCL	Brown-headed Nuthatch	BHNH	21
Foliage density at 1 m	FOLDN1	(*Sitta pusilla*)		
Foliage density at 3 m	FOLDN3	Carolina Wren	CWRN	81
Foliage density at 7–10 m	FOLDN8	(*Thryothorus*		
Foliage density at 12–15 m	FOLDN13	*ludovicianus*)		
Foliage density above 20 m	FOLDN20	White-eyed Vireo	WEV	65
% hardwoods 5–16 cm DBH	PHDW1	(*Vireo griseus*)		
% hardwoods 17–32 cm DBH	PHDW2	Red-eyed Vireo	REV	26
% hardwoods >32 cm DBH	PHDW3	(*V. olivaceus*)		
% pines 5–16 cm DBH	PPIN1	Black-and-white Warbler	BWW	41
% pines 17–32 cm DBH	PPIN2	(*Mniotilta varia*)		
% pines >32 cm DBH	PPIN3	Pine Warbler	PIW	69
No. tree stems 5–16 cm DBH	TRDN1	(*Dendroica pinus*)		
No. tree stems 17–32 cm DBH	TRDN2	Prairie Warbler	PRW	23
No. tree stems >32 cm DBH	TRDN3	(*D. discolor*)		
		Yellow-breasted Chat	CHAT	43
		(*Icteria virens*)		
		Northern Cardinal	CARD	97
		(*Cardinalis cardinalis*)		
		Indigo Bunting	IB	27
		(*Passerina cyanea*)		

[a] N = number of grid points for habitat used by each bird species.

minimize edge effect. Forty-six to 49 systematically located grid points (50 m between points) were established in each study area. Birds in the eight study areas were censused by spot-mapping (International Bird Census Committee 1970) from 1 April–8 June 1975 using the grid points to maintain plotting accuracy. Data with sufficient sample sizes (at least 21 grid points of vegetation measurements per species and more than 10 different individual birds per species) for analyses were collected for 12 species of birds (Table 1).

Vegetation measurements were made at each of the grid points in all study areas (Table 1). Foliage density from the ground to 3 m height was measured with a 0.5 × 0.5-m gridded board (MacArthur and MacArthur 1961). Foliage density at 7–20 m from the ground was measured by sighting vertically through a 400 mm telephoto lens on a reflex camera over each grid point (MacArthur and Horn 1969). Foliage density higher than 20 m was estimated from the proportion of the vertically directed camera lens unobscured by foliage above 20 m.

Density and diameter of trees over 5 cm DBH were measured on 10 × 10-m plots. Density

of woody plants less than 5 cm in diameter and over 30 cm high was measured on 2 × 2-m plots at the 382 sample points.

Territories of singing males determined from census data were superimposed on the eight study area maps containing grid points. Vegetation measurements at points falling within the territory boundaries of males of a species were considered habitat used by that species and were compared, using a two-group DFA, with vegetation measurements for grid points not included in the territories. (See Table 1 for sample sizes: number of grid points of used habitat [N] plus number of grid points not included in species territories = 382.) One analysis was calculated for each of the 12 bird species. Prior probabilities for classification functions were adjusted for differences in group sample sizes. All 12 DFAs were significant (Mahalanobis D square, similar to a MANOVA, $P < 0.05$).

We calculated the correlation of the original vegetation variables to the discriminant axis (canonical variate) for each species (Timm 1975, Dueser and Shugart 1978). We used this technique because it evaluates the importance of each variable to the discrimination independent of intercorrelations among the original variables. Although we have used the $P < 0.01$ as a cut off level for inclusion of correlations (Table 2), significance level should not be the main criterion to evaluate the correlations; the direction and relative magnitude are more meaningful (Timm 1975).

A 12-group DFA was calculated with vegetation measurements of each bird species as a group. We compared results of this community ordination with the individual results of the two-group DFAs to see which provide a higher degree of habitat resolution and classification success (Tables 3 and 4).

Calculation of two-group DFAs for habitat classification (Table 5) was accomplished by using stepwise DFA which allowed only certain variables to enter (F to enter and be removed was 1.5—see BMDP7M, Dixon 1974). Intercorrelations among variables resulted in differences in the sets of variables entered in Table 5 and Table 2 in each species category.

Violation of the assumption of homogeneity of group dispersions (heterogeneity of variance-covariance matrices) is a matter of increasing concern with the application of DFA to habitat studies (Williams 1981). Because of the high probability of an inequality of group dispersions resulting from unequal group sample sizes, we recalculated all 12 DFAs again after log transformation of the data. DFAs with the log transformed data supported the original analyses completely. There was no change in either the direction or relative magnitude of the correlations of original variables to the 12 discriminant functions. Thus, we considered the original analyses to be acceptable (Pimentel 1979).

Evaluating the importance of habitat variables for species by two-group DFA has a potential problem. If a bird does not occupy one extreme of the habitat for at least one variable, the analysis and subsequent correlations to the discriminant axis may not be significant. Thus, habitats of species favoring "middle" portions on all habitat gradients are difficult to quantify with DFA. Also, interspecific territoriality may force a subordinate species to use sub-optimal habitat. In such a case, the accuracy of a DFA to indicate a species' preferred habitat would be reduced. Many territories of the bird species we studied overlapped within study areas. Thus, we did not notice any obvious examples of interspecific territoriality.

RESULTS AND DISCUSSION

Comparison of two-group and 12-group DFA.—A three dimensional ordination of the 12 species following the 12-group DFA revealed four general aggregations of bird species (Fig. 1). Pine Warblers and Brown-headed Nuthatches formed one group representing species using mature pine forests (Table 3). Prairie Warblers and Yellow-breasted Chats formed an

TABLE 2

CORRELATIONS OF ORIGINAL VARIABLES TO DISCRIMINANT AXES FOR SONGBIRDS IN EAST TEXAS PINE AND PINE-HARDWOOD FORESTS ($P < 0.01$)[a]

Variables	WEV	CHAT	PRW	CARD	IB	CWRN	CCHK	REV	BWW	TUF	PIW	BHNH
VEGHT	-.3414	-.7754	-.7037	-.5041	—	—	—	.5989	.5393	.7380	.4882	—
NSRSP	.7269	.3441	.4115	.3499	—	.7272	-.5284	.3771	.3819	.2661	—	-.3919
NTRSP	—	—	—	—	-.4380	—	—	.7078	.7139	.6307	—	-.3616
SRDEN	.7900	.5267	.6628	.2416	—	.5741	-.3765	—	—	.5744	—	-.3158
CANCL	-.5058	-.5518	-.5000	-.3529	-.5592	—	-.2844	.6198	.4007	—	—	—
FOLDN1	.5432	.5087	.5049	.2745	—	.2854	—	—	—	—	—	—
FOLDN3	.4303	.2782	—	.2812	—	.2898	—	—	.3167	—	-.2526	-.2966
FOLDN8	—	—	—	—	-.3512	—	—	.4480	.3724	.4120	—	—
FOLDN13	-.2748	-.2720	-.2454	-.2781	-.2796	—	.3212	.3747	—	.2627	—	—
FOLDN20	—	—	—	—	—	—	-.2753	.4061	.3006	.2778	—	—
PHDW1	—	—	—	—	-.4555	.5253	—	.6802	.5196	.5973	—	-.3228
PHDW2	—	—	—	—	—	—	—	.3864	—	.2772	—	—
PHDW3	—	—	—	—	—	—	—	.2747	.3953	—	—	—
PPIN1	—	.5855	.4171	.2936	.5362	—	-.4987	-.6514	-.3196	-.6318	-.4695	-.3216
PPIN2	-.4991	-.3445	-.3529	-.6925	—	-.4501	.3926	—	—	—	.6974	.6511
PPIN3	—	—	—	—	—	—	—	—	—	—	.2724	.2724
TRDN1	—	—	—	—	—	—	-.3696	—	—	—	—	—
TRDN2	-.6116	-.4373	-.4278	-.6589	-.3978	-.5471	—	—	—	—	-.4853	-.4979
TRDN3	—	-.2620	—	—	—	—	—	.4259	.2998	.3336	—	—

a See Table 1 for samples sizes of habitat used by each species.

TABLE 3
CORRELATIONS OF ORIGINAL VARIABLES TO THE FIRST THREE AXES IN A 12-GROUP DFA CALCULATED ON COMBINED DATA OF 12 SPECIES OF COMMON SONGBIRDS IN EASTERN TEXAS[a]

Habitat variable	DFA		
	I	II	III
VEGHT	.7473	.4247	—
NSRSP	−.3548	.4483	.4136
NTRSP	—	.7260	—
SRDEN	−.4499	—	.5577
CANCL	.4829	.4880	—
FOLDN1	−.4436	—	.3651
FOLDN3	—	—	—
FOLDN8	—	.4639	—
FOLDN13	.2697	—	—
FOLDN20	—	.3621	—
PHDW1	—	.6184	—
PHDW2	—	.2570	—
PHDW3	—	—	—
PPIN1	−.6429	−.3404	—
PPIN2	.6072	−.4439	.3093
PPIN3	—	—	—
TRDN1	−.2588	.3266	−.5701
TRDN2	.5586	—	—
TRDN3	.2648	—	—
Cumulative % of variation explained	54.2	82.0	87.2

[a] See Table 1 for variable codes.

aggregation of species using early succession vegetation. Black-and-white Warblers, Red-eyed Vireos, Tufted Titmice, and Carolina Chickadees formed a third aggregation of species using relatively mature pine-hardwood forest vegetation with the latter of the four species using pines more often. The general vegetation requirements of the above eight species can be inferred from the ordination (Fig. 1) and correlations of original variables to the first three discriminant functions (Table 3). However, the detail and ranking of each original variable's importance to individual species are not as clear with the 12-group analysis (Table 3) as they are with the 12 two-group DFAs (Table 2).

The fourth aggregation of species from the 12-group DFA demonstrates the poor resolution even more (Fig. 1). A description of the vegetation requirements of the White-eyed Vireo, Northern Cardinal, Indigo Bunting,

TABLE 4

PERCENTAGES OF CORRECT CLASSIFICATIONS OF BIRD SPECIES BY TWO-GROUP AND SEVERAL-GROUP DFA[a]

Species	Two-group DFA	12-group DFA
WEV	70.8%	10.7%
CHAT	81.5%	44.2%
PRW	82.5%	65.2%
CARD	62.9%	11.3%
IB	65.5%	40.7%
CWRN	63.5%	7.4%
CCHK	70.0%	13.5%
REV	75.5%	38.5%
BWW	73.9%	29.3%
TUF	74.2%	18.0%
PIW	81.5%	15.9%
BHNH	86.4%	71.4%
Mean percentage correctly classified	74.0%	30.5%

[a] See Table 1 for species codes.

and Carolina Wren based on the results of the 12-group DFA would mask any special vegetation requirements of individual species. Results from the two-group DFAs provide detailed descriptions of the requirements of each species and clearly demonstrate differences among the four species (Table 2).

Comparison of the percentages of cases correctly classified by the 12-group versus two-group DFAs further demonstrates the accuracy of the two-group analyses (Table 4). In all species the percentage of correctly classified cases was higher with the two-group DFAs than with the 12-group DFA.

Two-group DFA bird-vegetation associations.—Several bird species were associated with low shrubby vegetation. White-eyed Vireos, Yellow-breasted Chats, Prairie Warblers, and Northern Cardinals were in general positively associated with increasing density of shrub stems (SRDEN), foliage density from 0–1 m high (FOLDN1), percent sapling pines (PPIN1), and number of shrub species (NSRSP) (Table 2). These four bird species were negatively associated with increasing vegetation height (VEGHT), percent canopy closure (CANCL), foliage density 12–15 m (FOLDN13), percent of pole-size pines (PPIN2), and density of all pole-size trees (TRDN2). The number of tree species (NTRSP) was apparently not important to these early succession species. Northern Cardinals, Yellow-

TABLE 5

UNSTANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS, CONSTANTS, AND GROUP MEANS FOR SONGBIRD HABITAT IN EAST TEXAS[a]

Variables	WEV	CHAT	PRW	CARD	IB	CWRN	CCHK	REV	BWW	TUF	PIW	BHNH
VEGHT	—	-.0790	-.0848	-.0806	.0857	—	—	—	.0457	.0809	.0665	—
NSRSP	—	—	—	—	—	.2146	—	.1201	.0736	—	-.0553	-.0625
NTRSP	—	.1180	—	—	—	-.2152	-.2066	.2265	.3004	.1384	—	-.2036
SRDEN	.0409	.0229	.0407	—	—	—	—	—	—	—	—	—
CANCL	—	—	—	—	-1.9859	—	—	1.2002	—	—	—	—
FOLDN1	2.5212	—	—	—	—	—	—	—	—	2.4682	—	—
FOLDN3	8.004	4.9559	-6.4090	—	-8.0149	—	—	—	8.5661	—	—	—
FOLDN8	—	—	—	—	—	—	—	—	—	1.4996	-1.2069	—
FOLDN13	—	—	—	—	—	—	—	—	—	—	-1.8595	—
FOLDN20	—	—	—	—	—	—	-5.9180	—	—	—	—	-3.3350
PHDW1	—	—	—	.8561	—	—	—	—	—	—	—	—
PHDW2	—	—	—	—	—	—	—	—	—	—	—	—
PHDW3	—	.9558	—	-12.1573	—	—	—	—	9.7891	—	—	8.7564
PPIN1	—	—	—	—	—	—	-1.6810	-.9368	—	—	—	-.7590
PPIN2	—	—	—	-1.1678	—	—	1.7384	—	—	1.4061	3.3430	3.4441
PPIN3	—	—	—	-.9191	—	—	—	—	—	—	—	1.1175
TRDN1	—	-.0371	-.0283	—	—	—	—	—	—	—	-.0307	—
TRDN2	-.1570	—	—	-.1749	-.3838	-.1553	-.3921	—	—	-.2381	-.2606	-.2824
TRDN3	—	—	—	.9031	-.5150	—	—	—	—	—	—	—
Constant	-.7927	.2830	1.1792	1.3452	.6702	-.5387	1.9711	-.8559	-2.000	-1.9135	-.6265	.8534
Group means												
Used habitat	.6997	1.4355	1.6805	.5637	1.0075	.6634	.7106	1.2590	.9340	1.0552	1.1938	1.7695
Unused hab.	-.1430	-.1815	-.1073	-.1912	-.0764	-.1779	-.0760	-.0917	.1119	-.1584	-.2623	-.1026

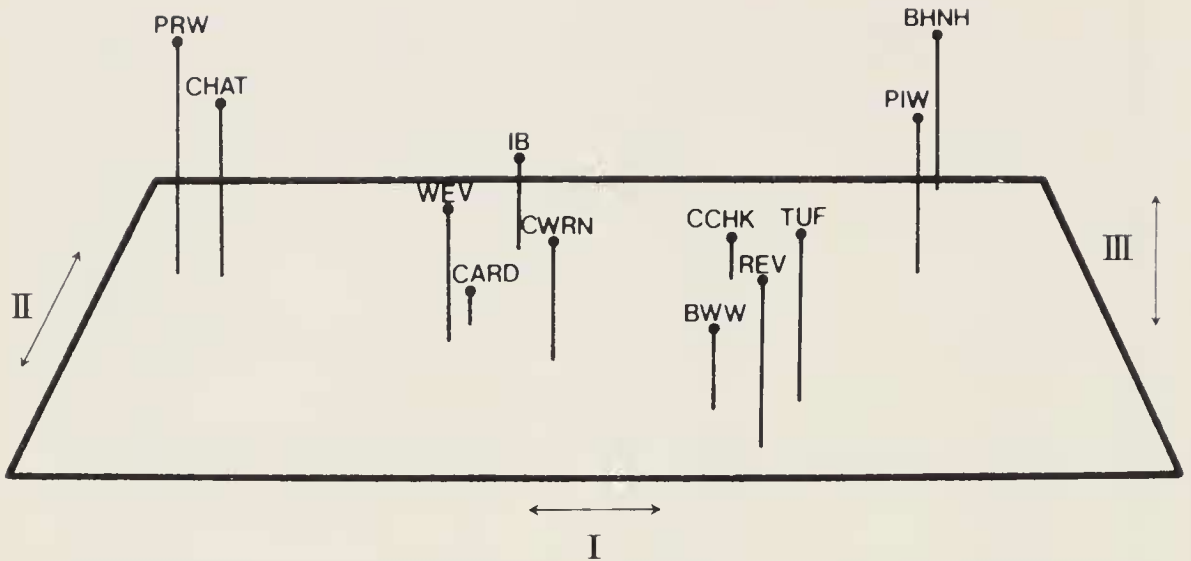[a] See Table 1 for sample sizes of habitat used by each species.

Fig. 1. Three dimensional ordination of a 12-group DFA on common East Texas song-birds. The first function (left to right) represents a transition from young clearcuts to mature forests. The second function (back to front) represents increasing tree and shrub species diversity. See Table 4 for correlations of original variables to axes and Table 1 for bird species codes.

breasted Chats, and White-eyed Vireos were positively associated with increasing foliage densities at 3 m (FOLDN3), as well as 1 m, above the ground and favored later phases of the early successional stage more than Prairie Warblers.

The above four bird species regularly use low, shrubby vegetation in other geographic areas. In Georgia, the same four species occurred in the grass-shrub stage of succession (Johnston and Odum 1956). Yellow-breasted Chats, Prairie Warblers, and Northern Cardinals were common breeding birds in 3-, 7-, and 12-year-old mixed oak stands in Virginia (Conner and Adkisson 1975), and the White-eyed Vireo occurred in the 7-year-old stand. In Arkansas, Prairie Warblers and Yellow-breasted Chats were characterized as open-country birds, and White-eyed Vireos inhabitated shrubs and low trees (James 1971). In East Texas, Northern Cardinals and White-eyed Vireos are ubiquitous and often occur in mature forests as well as clearcuts (Dickson and Segelquist 1979). In mature forests they probably occur where openings in the canopy permit shrub level vegetation.

Red-eyed Vireos, Black-and-white Warblers, and Tufted Titmice were associated with mature forest stands and were positively associated with increasing number of tree species, vegetation height, percent canopy closure, percent of sapling hardoods (PHDW1), large tree density (TRDN3), and number of shrub species (Table 2). The three bird species were neg-

atively affected by increasing percentages of sapling pines (i.e., young pine stands). In a study in Georgia, these three bird species were found only in the three oldest stands (Johnston and Odum 1956). In Arkansas they were typical inhabitants of well-developed shaded forests (James 1971). In another investigation in Arkansas, all had strong positive correlations with large trees, percent canopy cover, and average tree height (Smith 1977).

These three mature forest birds were also positively associated with increasing foliage density at 7–10 m (FOLDN8), 12–15 m (except Black-and-white Warblers) and above 20 m (FOLDN20). This association would be expected with Red-eyed Vireos as they are canopy gleaners (Williamson 1971). Anderson and Shugart (1974) found that Red-eyed Vireos were positively correlated with canopy biomass and subcanopy tree size.

Pine Warblers and Brown-headed Nuthatches were favored by mature stages of pine forests. Pine Warblers had strong positive associations with increasing percent of pole-size pines and vegetation height (Table 2). They avoided areas with dense sapling stage pines. The number of tree and shrub species, as well as foliage density at different heights, had little importance to Pine Warblers. Johnston and Odum (1956) found these birds in all their sampled pine stands from 25–100 years old. Anderson and Shugart (1974) noted the species frequented areas with a dense canopy and sparse understory. Brown-headed Nuthatches had a strong preference for pole stage pure pine stands. They were strongly associated with increasing percent of pole-size pines and negatively associated with increasing number of shrub species, number of tree species, and density of sapling stems (TRDN1) (Table 2). In Georgia, Johnston and Odum (1956) found them in the oldest pine stands. They noted that Pine Warblers, Brown-headed Nuthatches, and Red-cockaded Woodpeckers (*Picoides borealis*) were the only breeding species generally restricted to southern pines.

Indigo Buntings were somewhat similar to early succession species; however, they showed no relationship with vegetation height, number of shrub species, and density of shrub stems (Table 2). They were positively associated with increasing percentage of sapling pines, and negatively associated with increasing density of pole-size trees (TRDN2), density of foliage 7–15 m, number of tree species, and percent canopy closure. Indigo Buntings could apparently tolerate tall vegetation as long as it was sparse, i.e., very patchy. The absence of tall trees did not affect the bunting negatively. Indigo Buntings are sometimes abundant in both middle-aged and young shrubby stands in the south (Shugart and James 1973, Conner and Adkisson 1975, Strelke and Dickson 1980).

Carolina Wrens had strong positive associations with increasing number of shrub species, number of shrub stems, and percent sapling hardwoods

(Table 2). They were adversely affected by increasing density of pole-size trees and percent pines of pole size. Dense pole stands probably impeded light penetration and inhibited dense and diverse shrub level vegetation. Carolina Wrens, like Northern Cardinals and White-eyed Vireos, were found in a wide range of stand heights, but inhabited the shrub layer of vegetation. Carolina Wrens were positively associated with shrub level vegetation in Arkansas (James 1971) and Louisiana (Dickson and Noble 1978).

Carolina Chickadees preferred areas with open understories. They were negatively associated with increasing number of shrub species, shrub density, percent pine saplings and sapling density. They were positively associated with foliage density 12–15 m and percent of pole-size pines. Carolina Chickadees inhabited this pine and hardwood subcanopy, and the dense subcanopy probably shaded sufficient light to minimize understory growth beneath. Chickadees were found predominantly in the canopy of a mature hardwood forest in Louisiana (Dickson and Noble 1978), and in Georgia they inhabited the four oldest stands (Johnston and Odum 1956). In Virginia they inhabited two young stands (Conner and Adkisson 1975) and they were abundant in woods-clearcut edge in East Texas (Strelke and Dickson 1980). In Tennessee they also preferred habitat with open understories (Anderson and Shugart 1974).

Habitat classification.—Discriminant function analysis can be used to determine whether vegetation in different parts of a forest is suitable for a particular bird. Unstandardized discriminant function coefficients and constants (Table 5) can be used to calculate values that in turn can be used to evaluate the suitability of a particular forest area to the 12 bird species we studied.

The equation needed to evaluate each species is:

$$D = b_1X_1 + b_2X_2 + b_3X_3 + \ldots + b_iX_i + K$$

where D = the discriminant score needed to evaluate the species, b = the coefficients for each species' variables, X = the values for field measured habitat variables, and K = a constant for each species.

The discriminant score (D) is compared to a linear scale of the mean for habitat used by the species and the mean for habitat not used by the species. The closer the discriminant score is to the mean for used habitat, the more favorable the habitat is to the bird species being tested. Generally, the habitat in question would be considered favorable to the bird species if the discriminant score were greater than the midpoint between the means of the used and unused habitats (Conner and Adkisson 1976).

The habitat classification functions for only the White-eyed Vireo, Yellow-breasted Chat, Indigo Bunting, and Red-eyed Vireo were tested with

vegetation data collected in spot-mapped territories for each of these species during 1980. Data for the tests were collected on an area different from the original eight study areas. The averages of vegetation variables measured at three randomly located points within one territory of each species were used as input data for the habitat classifications. For example in the case of the Red-eyed Vireo ($b_i \times X_i$):

    NSRSP: $0.1201 \times 4.33 = 0.5200$
    NTRSP: $0.2265 \times 4.0 = 0.9060$
    CANCL: $1.2002 \times 0.9433 = 1.1321$
    PPIN1: $-0.9368 \times 0.0 = 0.0$

The sum of these products plus the constant (K = -0.8559) provides the discriminant score (D = 1.7022). For the Red-eyed Vireo the mean for the used habitat is 1.2590 and for the unused habitat -0.0917 (Table 5). Thus, the calculated discriminant score is much closer to the mean for habitat used by this species than the mean for habitat not used, and the area being tested would be correctly classified as habitat suitable for Red-eyed Vireos.

Discriminant scores calculated for the White-eyed Vireo (D = 2.1603), Yellow-breasted Chat (D = 1.6045), and Indigo Bunting (D = 0.4782) were closer to the mean for habitat used by the species than habitat not used (Table 5) and thus were all correctly classified.

MANAGEMENT RECOMMENDATIONS

Clearcutting in mixed pine-hardwood forests of East Texas provides excellent habitat for early succession bird species, such as White-eyed Vireos, Yellow-breasted Chats, Prairie Warblers, Northern Cardinals, and Indigo Buntings. Cuts 10–20 ha would be sufficient to contain at least several territories for each species. Buntings and Northern Cardinals also prefer some tall live or dead trees for singing perches. These birds need foliage 1–3 m above the ground for both foraging substrate and nest concealment. Indigo Buntings, however, would probably be tolerant of stands with low foliage density at 1 and 3 m. Shrub species diversity and stem density should be kept reasonably high to provide habitat for all of the five bird species. These requirements preclude or minimize the use of herbicides to eliminate young sprouting hardwoods. Clearcutting should provide high quality habitat for the birds for about 2–8 years after cutting.

Carolina Wrens, White-eyed Vireos, and Northern Cardinals inhabit shrub-level vegetation in stands of a wide variety of tree heights. In young pine stands, habitat for these birds could be enhanced by avoiding timber stand improvement (TSI, killing unwanted hardwoods), by planting with wide spacing such as 3.6 × 3.6 m (12 × 12 feet) and by avoiding intensive

site preparation measures such as KG blading and chopping. In old pole and mature stands, frequent thinnings and selected tree injection or girdling should enhance shrub vegetation.

Red-eyed Vireos, Black-and-white Warblers, and Tufted Titmice selected more mature forest stages. Later stages of forest succession (30–60 years following clearcutting), when trees are tall and at least a partly deciduous canopy is present, should provide high quality habitat. Since these three species used habitat with increasing tree species diversity, TSI should be avoided. Johnston and Odum (1956) and Dickson and Segelquist (1979) have pointed out the importance of deciduous foliage in pine stands to birds.

Carolina Chickadees, Pine Warblers, and Brown-headed Nuthatches selected pine pole stands and mature pine forests. Brown-headed Nuthatches in particular would benefit from management that provided mature stands of mostly pines. These three species would be negatively affected by clearcutting for perhaps 12–25 years.

SUMMARY

In 1975, 12 breeding bird species were spot-mapped in four pine stands of different heights and four comparable sized pine-hardwood stands. Vegetation measurements were made at 382 grid points within the eight stands. Vegetation at grid points within each species' territories was compared to vegetation not included in territories using a separate two-group discriminant function analysis (DFA) for each species. Correlations of original variables to the 12 DFA axes were calculated to determine which vegetation parameters were important to individual bird species. When compared to a single 12-group DFA, the two-group DFAs provided a more detailed description of individual species' vegetation requirements. Early succession bird species such as White-eyed Vireos, Yellow-breasted Chats, Prairie Warblers, and Northern Cardinals were positively associated with increasing density of shrub stems, foliage volume at 1 and 3 m high, percent sapling pines, and number of shrub species and negatively associated with increasing vegetation height, canopy closure, and number of pole-size trees. Late succession bird species such as Red-eyed Vireos, Black-and-white Warblers and Tufted Titmice favored increasing vegetation height, number of tree species, and canopy closure. Other bird species had their own specific vegetation requirements.

ACKNOWLEDGMENTS

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